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A comparative scanning electron microscope study of leaf surface morphology and anatomy for four species of Abronia found within California

Elliott Helm

A COMPARATIVE SCANNING ELECTRON MICROSCOPE STUDY OF LEAF SURFACE MORPHOLOGY AND ANATOMY FOR FOUR SPECIES OF *ABRONIA* FOUND WITHIN CALIFORNIA

A Thesis

Presented to the

Faculty of

California State

College, San Bernardino

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Biology

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by

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ABSTRACT

Large and small leaves of four species of *Abronia* Juss. found within California were studied to determine whether leaf surface morphology and anatomy can be correlated to habitat environmental conditions. Major characters considered include trichome and stomatal densities, vascular bundle, palisade cell, spongy cell, epidermal cell, trichome, and stomatal sizes.

Anatomical comparisons made between large and small leaves within individual species indicate no significant anatomical differences among leaf sizes for *Abronia villosa* var *aurita* (Abrams) Jeps., *Abronia nana* ssp. *covillei* (Heimerl) Munz, var *Abronia alpina* Bdg. Considerable anatomical difference exists between large and small leaves of *Abronia maritima* Nutt. ex Wats. A scanning electron microscope comparison of surface morphology for adaxial and abaxial surfaces of large and small leaves within individual species indicates no significant difference among leaf surface or sizes. There is a considerable anatomical and morphological difference among the leaves of the four species when compared collectively.

The smaller size of most major anatomical characters coupled with large relative amounts of palisade parenchyma, high stomatal densities, and diminutive amounts of spongy parenchyma within the leaves of A. *villosa* var *aurita*, A. *nana* ssp. *covillei*, and notably A. *alpina* are characteristic of

plants occupying xerophytic habitats. Enlargement of most major anatomical characters including large, well developed spongy parenchyma and low stomatal densities constitute a mesophytic leaf structure for A. *maritima*.

Relative sizes and numbers of trichomes could not be correlated to environmental conditions within the habitats of the four *Abronia* species studied.

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INTRODUCTION

The genus *Abronia* Juss. of the family Nyctaginaceae is represented in California by nine species of annual and perennial herbs, all of which are restricted to sandy, well-drained soils (Wilson 1972). The species are found within a diversity of habitats such as alpine meadows e.g., *Abronia alpina* Bdg., montane slopes e.g., *Abronia nana* Wats. ssp. *covillei* (Heimerl.) Munz, desert roadsides e.g., *Abronia villosa* var *aurita* (Abrams.) Jeps., and coastal fore-dunes e.g., *Abronia maritima* Nutt. ex Wats.

Because the species grow in ecologically distinct habitats, they are subjected to unique environmental stresses which result in a wide spectrum of morphological and anatomical diversity. This diversity has largely been ignored except for taxonomic considerations, e.g. Tillett (1967).

Recently, Wilson (1972, 1974, 1975) studied distribution, ecology, habit, anthocarp polymorphism and anatomy, and pericarp and seed coat anatomy of *Abronia* found in California. Her studies were focused on the ecological implications of anatomical and morphological modifications found within structures associated with reproductive and dispersal mechanisms of *Abronia*.

Adaptive modifications can be found within most plant organ systems. Because the leaf is an organ notably responsive to environmental stresses, many studies have been focused

on leaf anatomy and morphology. A few exceptional studies involving classical anatomy include Shields (1950), Ashby (1948), and Clements (1905). More recent studies focusing on anatomy and anatomical physiology include Mortenson (1973), Johnson (1975), Sharma (1975 b), Hsiao (1973), and Patel et al. (1975).

Abronia species are well-suited for study because they occupy habitats that are xeric to more mesic. An attempt will be made in this paper to correlate the ecological differences of these habitats with the anatomical and morphological modifications found within the leaves of four *Abronia* species. There are significant differences in the character of major structures, cells, and tissue systems within the leaves of the four *Abronia* species. These differences are hypothesized to be adaptive modifications resulting from unique selective pressures within the ecologically distinct habitats of the four species studied.

MATERIALS AND METHODS

Unless otherwise indicated, plant materials were collected during the summer of 1975 by the author and were preserved either as pressed voucher specimens or stored in a standard FAA solution (Johansen 1940). Species were delimited according to Munz (1974).

The following voucher specimens have been deposited at California State College San Bernardino: The montane species *Abronia nana* ssp. *covillei* number 1 was collected in the San Bernardino mountains at an elevation of 7,000 feet near the north shore of Big Bear Lake, San Bernardino County. *Abronia alpina* number 1296 was collected by Wilson in 1969 (Wilson 1972), in Ramshaw Meadows at an elevation of 8,000 feet, Tulare County. The desert species *Abronia villosa* var *aurita* number 2 was collected two miles north of Hemet at an elevation of 2,000 feet, Riverside County. The coastal species *Abronia maritima* number 6 was collected from the fore-dune at Oso Flaco Beach, San Luis Obispo County.

Leaves were taken from each of four representative plants selected from collections of A. *maritima*, A. *villosa* var *aurita*, and A. *nana* ssp. *covillei* populations. Because of the rarity of A. *alpina* (Wilson 1970), leaves were taken from only one specimen.

For all species of *Abronia*, there is a marked leaf dimorphism; one large and one small leaf located at the same

node (Fig. 1). "Large-small" leaf pairs located approximately midway on a main stem were excised from each plant in order to standardize leaf sampling.

To distinguish adaxial and abaxial surfaces for observation with the AMR 1000 Scanning Electron Microscope (SEM), the leaves were cut into asymmetrical segments (Fig. 2). These asymmetrical segments were dehydrated with an ethanol series (Falk, et al. 1971). During critical point drying, ethanol was replaced with CO_2 utilizing the Boman SP6-900 Critical Point Dryer. The CO_2 was expelled under critical heat and pressure which maintained the tissue's natural shape.

Next, a thin layer of 60% gold-palladium was applied to the leaf surfaces using a Kinney High-Vacuum Evaporator Model SC-3.

Data were collected from 4x5 negatives and from direct observations of the SEM scanning screen.

Stomatal and trichome densities were determined by counting the number of each observed within a 25 cm^2 quadrat placed on a 200 magnification negative. The numbers were converted to number per cm^2 by mathematically compensating for magnification and quadrat size. Two quadrats per leaf surface were taken.

Percentage of glandular trichomes was determined for each leaf surface by observing four full screen quadrats at 500 magnification.

Stomata were measured directly from the SEM scanning

screen at a magnification of 2,000, and reported in μ. Stomatal lengths and widths were determined by measuring the longest and then widest open space between the surrounding cuticular edges for five stomata per leaf surface.

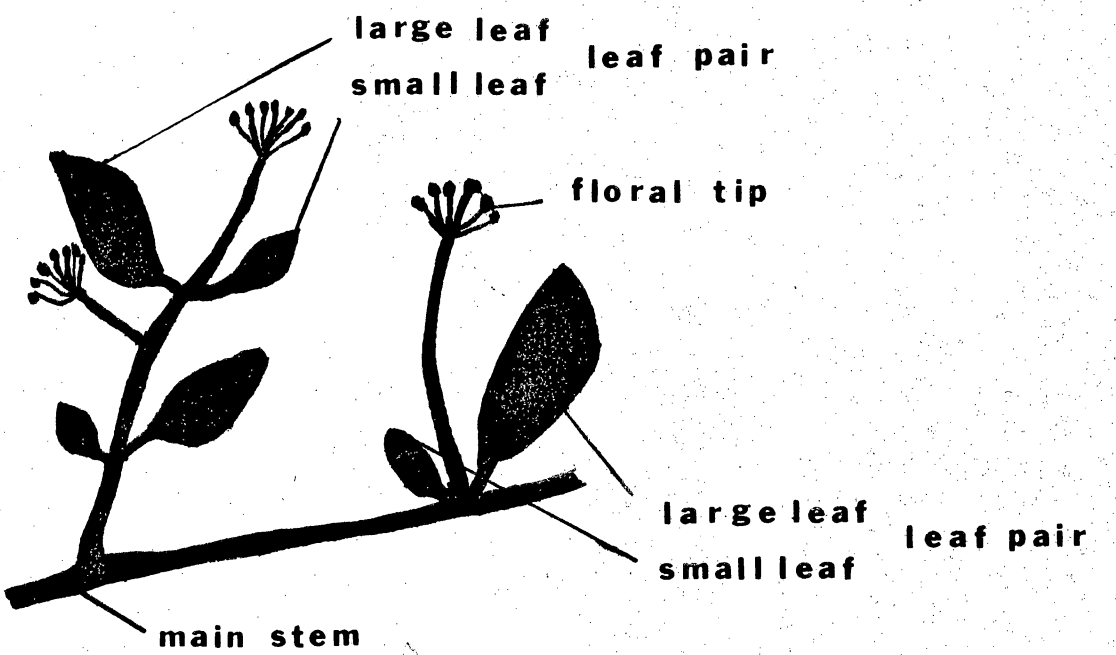
Because abundant trichomes hindered observation of stomata on the leaves of A. *maritima*, the apical portions of the trichomes were removed with a razor blade prior to gold coating.

Transections of leaves were prepared using the paraffin method and stained with Toluidine-blue O (Johansen 1940). Nineteen anatomical characters were measured in mm for each species. Major characters include epidermal cell height and width, palisade cell height and width, vascular bundle, and spongy cell dimensions. Also noted was the general arrangement of tissue types and relative amounts of intercellular spaces.

All anatomical and morphological data collected from both the SEM and paraffin transections were compared utilizing mean, standard deviation, and t-tests, calculated by the computer program SPSS.

Fig. 1. Generalized stem section of Abronia illustrating leaf dimorphism.

Fig. 2. Asymmetrical segments of a leaf used to distinguish adaxial and abaxial surfaces for SEM analysis.



1

adaxial surface

abaxial surface

2

RESULTS

Large and small leaves from four species of *Abronia* were analyzed for 26 anatomical and morphological characters. The results are presented in Tables 1-11 and Fig. 3-27.

A list of values for anatomical and morphological characters derived from leaf transections is presented in Tables 1-4. Within a single species, character size generally increases from small to large leaf. This is especially noticeable for leaf thickness (Tables 1-4). However, for some characters such as epidermal cell height and width (Tables 2 & 3), and vascular bundle height and width (Table 3), this trend is not clear-cut.

When the leaves of all species are compared, major anatomical characters including leaf thickness, adaxial and abaxial epidermal cell height, palisade cell height and width, and vascular bundle height and width are generally found to be largest for *Abronia maritima*, followed by *Abronia villosa* var *aurita*, *Abronia nana* ssp. *covillei*, and lastly, *Abronia alpina* (Tables 1-4). The above trend is somewhat variable for a few characters when the leaves of A. *villosa* var *aurita* and A. *nana* ssp. *covillei* are compared (Tables 2 & 3). An interesting deviation from the above major character trend is seen when small leaves are compared with each other. Adaxial epidermal cells are thickest for leaves of A. *villosa* var *aurita*, followed by A. *nana* ssp. *covillei*, A. *maritima*, and

A. alpina.

Relative amount of palisade tissue is greatest for leaves of *A. alpina*, followed by *A. nana* ssp. *covillei*, *A. villosa* var *aurita*, and *A. maritima* (Tables 1-4 and Fig. 3-6). Palisade tissue nearly traverses the entire leaf thickness for *A. alpina*, *A. nana* ssp. *covillei*, and *A. villosa* var *aurita*, while being bilaterally situated in leaves of *A. maritima* (Fig. 5).

Trichome character values including adaxial and abaxial trichome height, width, and number of cells per trichome for both large and small leaves are generally largest within *A. villosa* var *aurita*, followed by *A. maritima*, *A. alpina*, and lastly *A. nana* ssp. *covillei* (Tables 1-4).

General reduction of anatomical characters is noted for both leaf sizes of *A. alpina* (Table 4).

Table 9 lists t-test results for comparisons of anatomical and morphological characters derived from transections of large and small leaves of the four *Abronia* species studied. With a 98% confidence level, t-tests indicate no significant difference between the majority of characters within the large or small leaves for any single species except *A. maritima*. A considerable difference in character sizes occurs between the large and small leaves of *A. maritima*. A comparison of characters among the leaves of different species indicates that the majority of characters are significantly different. A few characters such as epidermal cell

dimensions and cells per trichome show some degree of continuity among the species.

Representative leaf transections for the four *Abronia* species studied are shown in Fig. 3-6.

A general reduction in size of major anatomical characters including leaf thickness, palisade cell, spongy cell, and vascular bundle dimensions within the leaf of A. *alpina* is evident in Fig. 3. Palisade tissue overlaps and traverses the entire leaf thickness resulting in little intercellular space.

Similarity of anatomical structure for leaves of A. *villosa* var *aurita* and A. *nana* ssp. *covillei* is shown in Fig. 4 & 6. Leaf thickness, palisade cell, spongy cell, and vascular bundle dimensions are somewhat comparable in size. Due to the similarity of palisade tissues, the relative amount of intercellular space is also comparable between the two species. However, trichomes are very different in size.

The large size of most anatomical characters for the leaves of A. *maritima* is illustrated in Fig. 5. There is a notable increase in size and amount of spongy mesophyll tissue, partially due to the reduction of palisade tissue to a bilateral rather than a transverse position. The replacement of spongy mesophyll with palisade tissue is not evident for the leaves of A. *maritima*.

When values for morphological characters derived from SEM analysis of abaxial and adaxial surfaces of large

and small leaves of the four *Abronia* species are considered (Tables 5-8), there is no apparent trend indicating that character quality is influenced by either leaf size or surface placement. The highest character values are equally divided between large and small leaves, and abaxial and adaxial surfaces. Likewise, the lowest character values are also divided equally between large and small leaves and nearly equally between adaxial and abaxial surfaces. However, trends are evident with regard to the placement of some individual characters. Both stomata and trichome densities are normally found to be highest on small leaves (Tables 5, 6, & 7), and stomatal dimensions appear largest on the large leaves (Tables 6, 7, & 8). Contrary to what might be expected, stomatal densities appear not to be influenced by surface placement, yet trichome densities are found to be higher on abaxial leaf surfaces (Tables 5, 6, & 8).

A comparison of morphological characters among the four species of *Abronia* indicates that for all leaf sizes and surfaces, A. *alpina* has the highest stomatal densities (Table 8), A. *maritima* has the highest trichome densities (Table 5), A. *villosa* var *aurita* has the highest stomata/trichome ratio and greatest percentage of glandular trichomes (Table 6), and A. *nana* ssp. *covillei* has the largest stomata (Table 7).

For both large and small leaves and adaxial and abaxial surfaces, stomata/cm^2 is highest for A. *alpina*,

followed by A. *villosa* var *aurita*, A. *nana* ssp. *covillei*, and lastly A. *maritima*. This is an example of major morphological character following an absolute trend (Tables 5-8). Trichomes/cm^2 for small leaves is highest within A. *alpina maritima*, followed by A. *nana* ssp. *covillei*, and A. *villosa* var *aurita*. Trichome density for large leaves deviates slightly from the above trend, having A. *maritima*, followed by A. *alpina*, A. *nana* ssp. *covillei*, and A. *villosa* var *aurita*.

Generally, stomatal dimensions for small leaves are largest for A. *nana* ssp. *covillei*, followed by A. *maritima*, A. *villosa* var *aurita*, and A. *alpina* (Tables 5-8). There is no appreciable trend regarding stomatal sizes for large leaves of the *Abronia* species.

T-test comparisons of data on morphological characters taken from SEM analysis of abaxial and adaxial surfaces of large and small leaves for the four *Abronia* species is presented in Tables 10 & 11. They indicate that within a single species, there is no significant difference in character values for large or small leaves nor abaxial or adaxial surfaces. A comparison of characters among different species shows that in most cases, the character values are significantly different. However, stomatal length or width for example, show some degree of continuity among the different species.

Fig. 7-14 illustrate general surface morphology for adaxial and abaxial surfaces of the four *Abronia* species.

Striking differences in trichome and stomatal densities among the *Abronia* species are shown in these figures. Fig. 7 & 8 show the high stomatal/trichome ratio for A. *villosa* var *aurita*, while Fig. 11 & 12 show the great amount of trichomes on the leaves of A. *maritima*, resulting in a low stomatal/trichome ratio. Fig. 9 & 10 illustrate the nearly 1 to 1 ratio of stomata to trichomes for A. *nana* ssp. *covillei* leaves. Similarity of general surface morphology between abaxial and adaxial leaf surfaces is shown for A. *nana* ssp. *covillei* (Fig. 9 & 10), A. *maritima* (Fig. 11 & 12), and A. *alpina* (Fig. 13 & 14). These species have similar trichome and stomatal densities as well as comparable trichome structure between their adaxial and abaxial sides. *Abronia villosa* var *aurita* is shown to have notable differences between adaxial and abaxial trichome structure (Fig. 7 & 8).

Fig. 15-19 illustrate the variability of trichome morphology found within the four *Abronia* species. Fig 15 & 16 show the difference of trichome morphology between adaxial and abaxial leaf surfaces of A. *villosa* var *aurita*. The adaxial trichomes have a greatly expanded basal cell, while the abaxial trichomes are linear and lack an expanded basal cell. Trichomes of A. *maritima* (Fig. 17), A. *nana* ssp. *covillei* (Fig. 18), and A. *alpina* (Fig. 19), are linear, uniseriate, and smaller in stature than the trichomes of A. *villosa* var *aurita* (Fig. 15 & 16). A considerable percentage of trichomes for all the *Abronia* species studied are

shown to be capitate or glandular (Fig. 15-19). There is little diversity among trichomes or any given leaf surface for A. *maritima*, A. *nana* ssp. *covillei* and A. *alpina*, while significant diversity exists between trichomes on A. *villosa* var *aurita*.

Similarity in stomatal morphology for abaxial and adaxial leaf surface of the four *Abronia* species studied is evident (Fig. 20-27). All stomatal structures have a cuticular edge surrounding the aperture, which probably remains open during guard cell fluctuations. There appears to be some folding of the cuticular edge in a few cases, e.g. A. *nana* ssp. *covillei* (Fig. 22 & 23), which might indicate slight cuticular edge movement. Most stomatal apertures are slightly recessed within the epidermal layer, although no stomatal crypts are present.

Table 1. Values[a] of anatomical and morphological characters for large and small leaves of *Abronia maritima* populations from Oso Flaco Beach, San Luis Obispo Co.

Anatomical/Morphological Characters	small leaf			large leaf		
	mean	S.D.	N	mean	S.D.	N
Leaf thickness at bundle	1.552	0.431	8	2.251	0.294	8
Leaf thickness not at bundle	1.417	0.114	8	1.907	0.496	8
Adaxial epidermal cell height	0.027	0.004	24	0.036	0.007	24
Adaxial epidermal cell width	0.030	0.005	24	0.038	0.007	24
Abaxial epidermal cell height	0.026	0.004	24	0.032	0.005	24
Abaxial epidermal cell width	0.028	0.004	24	0.035	0.006	24
Palisade cell height	0.154	0.045	24	0.330	0.166	24
Palisade cell width	0.034	0.011	24	0.062	0.030	24
Number of layers of palisade	2.62	0.74	8	4.37	2.20	8
Spongy cell diameter	0.119	0.031	24	0.154	0.059	24
Crystals, number per section	94.50	6.67	8	98.37	6.80	8
Major bundle height	0.213	0.044	8	0.237	0.031	8
Major bundle width	0.225	0.060	8	0.252	0.051	8
Adaxial trichome height	0.106	0.009	16	0.115	0.015	16
Adaxial trichome width	0.028	0.005	16	0.030	0.004	16
Abaxial trichome height	0.104	0.013	16	0.125	0.017	16
Abaxial trichome width	0.023	0.012	16	0.028	0.007	16
Number of cells per adaxial trichome	5.43	0.89	16	5.62	1.31	16
Number of cells per abaxial trichome	5.56	0.72	16	5.81	1.37	16

[a]Measurements taken from transections of large and small leaves located midway on a main stem, and are in mm.

Table 2. Values[a] of anatomical and morphological characters for large and small leaves of *Abronia villosa* var *aurita* populations from Hemet, Riverside Co.

Anatomical/Morphological Characters	small leaf			large leaf		
	mean	S.D.	N	mean	S.D.	N
Leaf thickness at bundle	0.650	0.128	8	0.686	0.144	8
Leaf thickness not at bundle	0.476	0.040	8	0.490	0.044	8
Adaxial epidermal cell height	0.037	0.007	24	0.036	0.007	24
Adaxial epidermal cell width	0.041	0.011	24	0.042	0.011	24
Abaxial epidermal cell height	0.030	0.006	24	0.029	0.006	24
Abaxial epidermal cell width	0.032	0.006	24	0.033	0.010	24
Palisade cell height	0.124	0.019	24	0.120	0.018	24
Palisade cell width	0.023	0.004	24	0.023	0.003	24
Number of layers of palisade	3.50	.53	8	3.25	0.88	8
Spongy cell diameter	0.041	0.015	24	0.043	0.015	24
Crystals, number per section	101.87	14.99	8	116.87	26.78	8
Major bundle height	0.152	0.035	8	0.175	0.29	8
Major bundle width	0.141	0.052	8	0.195	0.066	8
Adaxial trichome height	0.299	0.059	16	0.322	0.093	16
Adaxial trichome width	0.056	0.026	16	0.055	0.015	16
Abaxial trichome height	0.268	0.095	16	0.246	0.059	16
Abaxial trichome width	0.041	0.021	16	0.042	0.019	16
Number of cells per adaxial trichome	6.18	0.98	16	5.62	0.80	16
Number of cells per abaxial trichome	6.06	1.12	16	6.06	1.12	16

[a]Measurements taken from transections of large and small leaves located midway on a main stem, and are in mm.

Table 3. Values[a] of anatomical and morphological characters for large and small leaves of *Abronia nana* ssp. *covillei* populations from Big Bear Lake, San Bernardino Co.

Anatomical/Morphological Characters	small leaf			large leaf		
	mean	S.D.	N	mean	S.D.	N
Leaf thickness at bundle	0.616	0.068	8	0.631	0.061	8
Leaf thickness not at bundle	0.602	0.045	8	0.611	0.025	8
Adaxial epidermal cell height	0.034	0.005	24	0.032	0.006	24
Adaxial epidermal cell width	0.035	0.006	24	0.033	0.004	24
Abaxial epidermal cell height	0.029	0.005	24	0.028	0.005	24
Abaxial epidermal cell width	0.030	0.007	24	0.031	0.007	24
Palisade cell height	0.119	0.022	24	0.125	0.014	24
Palisade cell width	0.019	0.005	24	0.017	0.004	24
Number of layers of palisade	5.25	0.70	8	5.25	0.70	8
Spongy cell diameter	0.032	0.011	24	0.031	0.009	24
Crystals, number per section	48.62	6.09	8	57.75	4.02	8
Major bundle height	0.191	0.022	8	0.171	0.024	8
Major Bundle width	0.162	0.027	8	0.147	0.035	8
Adaxial trichome height	0.071	0.013	16	0.085	0.014	16
Adaxial trichome width	0.019	0.002	16	0.020	0.005	16
Abaxial trichome height	0.076	0.016	16	0.076	0.015	16
Abaxial trichome width	0.018	0.003	16	0.018	0.003	16
Number of cells per adaxial trichome	3.87	0.50	16	4.00	0.54	16
Number of cells per abaxial trichome	4.06	0.77	16	3.93	0.68	16

[a]Measurements taken from transections of large and small leaves located midway on a main stem, and are in mm.

Table 4. Values[a] of anatomical and morphological characters for large and small leaves of *Abronia alpina* from Ramshaw Meadows, Tulare Co.

Anatomical/Morphological Characters	small leaf			large leaf		
	mean	S.D.	N	mean	S.D.	N
Leaf thickness at bundle	0.302	0.005	4	0.352	0.005	4
Leaf thickness not at bundle	0.297	0.005	4	0.380	0.024	4
Adaxial epidermal cell height	0.022	0.003	12	0.023	0.003	12
Adaxial epidermal cell width	0.024	0.005	12	0.025	0.003	12
Abaxial epidermal cell height	0.019	0.003	12	0.018	0.003	12
Abaxial epidermal cell width	0.021	0.005	12	0.017	0.002	12
Palisade cell height	0.059	0.004	12	0.074	0.007	12
Palisade cell width	0.011	0.002	12	0.011	0.001	12
Number of layers of palisade	5.75	0.50	4	5.75	0.50	4
Spongy cell diameter	0.015	0.005	12	0.016	0.004	12
Crystals, number per section	29.00	3.65	4	26.25	3.77	4
Major bundle height	0.087	0.005	4	0.094	0.006	4
Major bundle width	0.105	0.019	4	0.085	0.006	4
Adaxial trichome height	0.105	0.014	8	0.106	0.017	8
Adaxial trichome width	0.017	0.005	8	0.016	0.005	8
Abaxial trichome height	0.100	0.008	8	0.103	0.016	8
Abaxial trichome width	0.017	0.005	8	0.020	0.005	8
Number of cells per adaxial trichome	4.25	0.70	8	4.37	0.51	8
Number of cells per abaxial trichome	4.12	0.35	8	4.37	0.51	8

[a]Measurements taken from transections of large and small leaves located midway on a main stem, and are in mm.

Table 5. Values[a] of morphological characters for large and small leaves of *Abronia maritima* populations from Oso Flaco Beach, San Luis Obispo Co.

Morphological Characters	small leaf			large leaf		
	mean	S.D.	N	mean	S.D.	N
Adaxial surface						
Stomata/cm^2	8991.66	1787.97	12	8258.16	1031.29	12
Trichomes/cm^2	32009.66	3526.39	12	31973.09	3544.40	12
Stomata/trichome	0.28	0.06	12	0.25	0.03	12
Stomatal length	12.76	3.11	30	12.89	2.88	30
Stomatal width	5.69	2.16	30	5.86	2.11	30
Stomatal length/width	2.52	1.14	30	2.40	0.93	30
Glandular trichomes, % of those counted	21.66	7.78	24	20.66	6.84	24
Abaxial surface						
Stomata/cm^2	8961.00	1094.89	12	8598.58	1485.70	12
Trichomes/cm^2	33583.91	2748.70	12	33209.08	3678.63	12
Stomata/trichome	0.26	0.04	12	0.25	0.04	12
Stomatal length	14.04	3.77	30	12.70	2.59	30
Stomatal Width	5.82	1.34	30	5.98	1.95	30
Stomatal length/width	2.30	0.51	30	2.25	0.54	30
Glandular trichomes, % of those counted	22.37	8.99	24	24.04	7.38	24

[a]Measurements taken from SEM micrographa and are in μ.

Table 6. Values[a] of morphological characters for large and small leaves of *Abronia villosa* var *aurita* populations from Hemet, Riverside Co.

Morphological Characters	small leaf			large leaf		
	mean	S.D.	N	mean	S.D.	N
Adaxial surface						
Stomata/cm^2	16257.08	3699.31	12	15410.83	3357.02	12
Trichomes/cm^2	3715.91	1303.05	12	3035.33	867.05	12
Stomata/trichome	4.60	1.32	12	5.83	1.65	12
Stomatal length	9.27	2.21	30	15.82	5.57	30
Stomatal width	5.15	1.78	30	7.47	1.70	30
Stomatal length/width	2.05	0.73	30	2.12	0.57	30
Glandular trichomes, % of those counted	91.58	12.88	24	88.12	14.76	24
Abaxial surface						
Stomata/cm^2	17485.82	3759.76	12	17320.75	4511.03	12
Trichomes/cm^2	4170.25	1437.71	12	3521.16	946.90	12
Stomata/trichome	4.44	1.28	12	5.18	1.71	12
Stomatal length	9.08	2.06	30	11.82	2.40	30
Stomatal width	4.31	1.43	30	4.96	1.30	30
Stomatal length/width	2.24	0.67	30	2.52	0.84	30
Glandular trichomes, % of those counted	97.50	5.05	24	92.58	10.11	24

[a]Measurements taken from SEM micrographs and are in μ.

Table 7. Values[a] of morphological characters for large and small leaves of *Abronia nana* ssp. *covillei* populations from Big Bear Lake, San Bernardino Co.

Morphological Characters	small leaf			large leaf		
	mean	S.D.	N	mean	S.D.	N
Adaxial surface						
Stomata/cm^2	14494.08	3208.18	12	13982.20	2756.20	12
Trichomes/cm^2	10868.16	2483.70	12	8638.08	2311.30	12
Stomata/trichome	1.34	0.23	12	1.66	0.32	12
Stomatal length	14.85	3.87	30	15.93	2.23	30
Stomatal width	5.29	2.12	30	4.98	1.53	30
Stomatal length/width	3.06	1.00	30	3.38	0.95	30
Glandular trichomes, % of those counted	64.83	18.93	24	58.54	16.22	24
Abaxial surface						
Stomata/cm^2	13091	2298.23	12	12814.66	2774.25	12
Trichomes/cm^2	9222.50	2053.54	12	8221.41	2560.81	12
Stomata/trichome	1.45	0.29	12	1.67	0.67	12
Stomatal length	14.04	3.77	30	15.31	3.78	30
Stomatal width	5.83	1.72	30	5.09	1.19	30
Stomatal length/width	2.65	0.70	30	3.19	1.29	30
Glandular trichomes, % of those counted	61.62	16.69	24	58.41	19.16	24

[a]Measurements taken from SEM micrographs and are in μ.

Table 8. Values[a] of morphological characters for large and small leaves of *Abronia alpina* from Ramshaw Meadows, Tulare Co.

Morphological Characters	small leaf			large leaf		
	mean	S.D.	N	mean	S.D.	N
Adaxial surface						
Stomata/cm^2	26042.50	950.60	4	25672.25	607.66	4
Trichomes/cm^2	9141.00	548.64	4	9089.50	491.07	4
Stomata/trichome	2.84	0.09	4	2.82	0.07	4
Stomatal length	7.84	3.20	10	14.88	1.76	10
Stomatal width	3.64	1.44	10	5.73	0.42	10
Stomatal length/width	2.15	0.36	10	2.11	0.46	10
Glandular trichomes, % of those counted	65.50	5.44	4	73.25	10.75	4
Abaxial surface						
Stomata/cm^2	26020.25	668.7	4	26605.75	617.14	4
Trichomes/cm^2	8994.00	159.34	4	9374.11	480.43	4
Stomata/trichome	2.88	0.08	4	2.83	0.14	4
Stomatal length	7.95	2.53	10	11.83	1.68	10
Stomatal width	3.37	2.08	10	5.69	1.06	10
Stomatal length/width	2.96	1.24	10	2.11	0.37	10
Glandular trichomes, % of those counted	72.75	5.12	4	73.00	3.65	4

[a]Measurements taken from SEM micrographs and are in μ.

Table 9. Comparison (using t-test values[a]) of anatomical and morphological characters among four species of *Abronia* for large and small leaves.

Anatomical/Morphological Characters	Species-leaf size vs. Species-leaf size	Mar-L vs. Mar-s	Mar-L vs. Vil-L	Mar-L vs. Vil-s	Mar-L vs. Nan-L	Mar-L vs. Nan-s	Mar-s vs. Vil-L	Mar-s vs. Vil-s	Mar-s vs. Nan-L	Mar-s vs. Nan-s	Vil-L vs. Vil-s	Vil-L vs. Nan-L	Vil-L vs. Nan-s
Leaf thickness at bundle		+	+	+	+	+	+	+	+	+	+	-	-
Leaf thickness not at bundle		+	+	+	+	+	+	+	+	+	-	+	+
Adaxial epidermal cell height		+	-	-	-	-	+	+	+	+	-	-	-
Adaxial epidermal cell width		+	-	-	+	-	+	+	-	-	-	+	+
Abaxial epidermal cell height		+	-	-	+	-	-	+	-	-	-	-	-
Abaxial epidermal cell width		+	-	-	-	+	-	-	-	-	-	-	-
Palisade cell height		+	+	+	+	+	+	+	+	+	-	-	-
Palisade cell width		+	+	+	+	+	+	+	+	+	-	+	+
Number of palisade layers		-	-	+	-	-	-	+	+	+	-	+	+
Spongy cell diameter		+	+	+	+	+	+	+	+	+	-	+	+
Crystals, number per section		-	-	-	+	+	-	-	+	+	+	+	+
Major bundle height		+	+	+	+	+	-	+	-	-	+	-	-
Major bundle width		-	-	+	+	+	-	+	+	+	+	-	-
Adaxial trichome height		-	+	+	+	+	+	+	+	+	+	+	+
Adaxial trichome width		-	+	+	+	+	+	+	+	+	-	+	+
Abaxial trichome height		+	+	+	+	+	+	+	+	+	+	+	+
Abaxial trichome width		+	+	+	+	+	+	+	-	-	-	+	+
Number of cells per adaxial trichome		-	-	-	+	+	-	-	+	+	-	+	+
Number of cells per abaxial trichome		-	-	-	+	+	+	-	+	+	-	+	+

[a]Key for the symbols and species abbreviations used in the above table.

Confidence level	Species	Leaf size
+ 98% or above	Mar - *maritima*	L - large leaf
- below 98%	Nan - *nana* ssp. *covillei*	s - small leaf
	Alp - *alpina*	
	Vil - *villosa* var *aurita*	

Table 9. continued

Anatomical/Morphological Characters	Species-leaf size vs. Species-leaf size	Vil-s vs. Nan-L	Vil-s vs. Nan-s	Nan-L vs. Nan-s	Alp-L vs. Alp-s
Leaf thickness at bundle		-	-	-	+
Leaf thickness not at bundle		+	+	-	+
Adaxial epidermal cell height		+	-	-	-
Adaxial epidermal cell width		+	+	-	-
Abaxial epidermal cell height		-	-	-	-
Abaxial epidermal cell width		-	-	-	+
Palisade cell height		-	-	-	+
Palisade cell width		+	+	-	-
Number of palisade layers		+	+	-	-
Spongy cell diameter		+	-	-	-
Crystals, number per section		+	+	+	-
Major bundle height		-	+	-	-
Major bundle width		-	-	-	-
Adaxial trichome height		+	+	+	-
Adaxial trichome width		+	+	-	-
Abaxial trichome height		+	+	-	-
Abaxial trichome width		+	+	-	-
Number of cells per adaxial trichome		+	+	-	-
Number of cells per abaxial trichome		+	+	-	-

Table 10. Comparison (using t-test values[a]) of morphological characters among three species of *Abronia* for large and small leaves.

Morphological Characters	Species-leaf size, surface vs. Species-leaf size	Mar-L AD vs. Mar-L	Mar-L AD vs. Mar-s	Mar-L AD vs. Vil-L	Mar-L AD vs. Vil-s	Mar-L AD vs. Nan-L	Mar-L AD vs. Nan-s	Mar-L ab vs. Mar-s	Mar-L ab vs. Vil-L	Mar-L ab vs. Vil-s	Mar-L ab vs. Nan-L	Mar-L ab vs. Nan-s	Mar-s AD vs. Mar-s	Mar-s AD vs. Vil-L	Mar-s AD vs. Vil-s	Mar-s AD vs. Nan-L	Mar-s AD vs. Nan-s
Adaxial surface																	
Stomata/cm^2			-	+	+	+	+	-	+	+	+	+		+	+	+	+
Trichomes/cm^2			-	+	+	+	+	-	+	+	+	+		+	+	+	+
Stomata/trichome			-	+	+	+	+	-	+	+	+	+		+	+	+	+
Stomatal length			-	+	+	+	-	-	+	+	+	+		+	+	+	-
Stomatal width			-	+	+	-	-	-	+	+	-	-		+	-	-	-
Stomatal length/width			-	-	-	+	+	-	-	-	+	+		-	-	+	-
Glandular trichomes, % of those counted			-	+	+	+	+	-	+	+	+	+		+	+	+	+
Abaxial surface																	
Stomata/cm^2		-	-	+	+	+	+	-	+	+	+	+	-	+	+	+	+
Trichomes/cm^2		-	-	+	+	+	+	-	+	+	+	+	-	+	+	+	+
Stomata/trichome		-	-	+	+	+	+	-	+	+	+	+	-	+	+	+	+
Stomatal length		-	-	-	+	+	-	-	-	+	+	-	-	-	+	+	-
Stomatal width		-	-	-	+	-	-	-	-	+	-	-	-	-	+	-	-
Stomatal length/width		-	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-
Glandular trichomes, % of those counted		-	-	+	+	+	+	-	+	+	+	+	-	+	+	+	+

[a]Key for the symbols and species abbreviations used in the above table.

Confidence level	Species	Leaf size	Leaf surface
+ 98% or above	Mar - *maritima*	L - large leaf	AD - adaxial
- below 98%	Nan - *nana* ssp. *covillei*	s - small leaf	ab - abaxial
	Vil - *villosa* var. *aurita*		

Table 10. continued

Morphological Characters	Species-leaf size, surface vs. Species-leaf size	Mar-s ab vs. Vil-L	Mar-s ab vs. Vil-s	Mar-s ab vs. Nan-L	Mar-s ab vs. Nan-s	Vil-L AD vs. Vil-L	Vil-L AD vs. Vil-s	Vil-L AD vs. Nan-L	Vil-L AD vs. Nan-s	Vil-L ab vs. Vil-s	Vil-L ab vs. Nan-L	Vil-L ab vs. Nan-s	Vil-s AD vs. Vil-s	Vil-s AD vs. Nan-L	Vil-s AD vs. Nan-s	Vil-s ab vs. Nan-L	Vil-s ab vs. Nan-s
Adaxial surface																	
Stomata/cm^2		+	+	+	+		-	-	-	-	-	-		-	-	+	-
Trichomes/cm^2		+	+	+	+		-	+	+	-	+	+		+	+	+	+
Stomata/trichome		+	+	+	+		-	+	+	-	+	+		+	+	+	+
Stomatal length		-	+	+	-		+	-	-	-	+	+		+	+	+	+
Stomatal width		+	-	+	-		+	+	-	-	-	-		-	-	-	-
Stomatal length/width		-	-	+	+		-	+	+	-	+	-		+	+	+	+
Glandular trichomes, % of those counted		+	+	+	+		-	+	+	-	+	+		+	+	+	+
Abaxial surface																	
Stomata/cm^2		+	+	+	+	-	-	+	+	-	+	+	-	+	-	+	+
Trichomes/cm^2		+	+	+	+	-	-	+	+	-	+	+	-	+	+	+	+
Stomata/trichome		+	+	+	+	-	-	+	+	-	+	+	-	+	+	+	+
Stomatal length		-	+	+	-	+	+	-	-	+	+	+	-	+	+	+	+
Stomatal width		+	+	-	-	+	+	+	+	-	-	-	-	-	-	-	-
Stomatal length/width		-	-	+	-	-	-	+	+	-	-	-	-	+	+	+	-
Glandular trichomes, % of those counted		+	+	+	+	-	+	+	+	-	+	+	-	+	+	+	+

Table 10. continued

Morphological Characters	Species-leaf size, surface vs. Species-leaf size	Nan-l AD vs. Nan-L Nan-s	Nan-L ab vs. Nan-s	Nan-s AD vs. Nan-s
Adaxial surface				
Stomata/cm^2		-	-	
Trichomes/cm^2		-	+	
Stomata/trichome		+	-	
Stomatal length		-	-	
Stomatal width		-	-	
Stomatal length/width		-	-	
Glandular trichomes, % of those counted		-	-	
Abaxial surface				
Stomata/cm^2	-	-	-	-
Trichomes/cm^2	-	-	-	-
Stomata/trichome	-	-	-	-
Stomatal length	-	-	-	-
Stomatal width	-	-	-	-
Stomatal length/width	-	+	-	-
Glandular trichomes, % of those counted	-	-	-	-

Table 11. Intraspecific comparison (using t-test values[a]) of leaf surface features for large and small leaves of *Abronia alpina* from Ramshaw Meadows, Tulare Co.

Morphological Characters	Leaf size-surface vs. leaf size-surface	Large-AD vs. Large-ab	Large-AD vs. small-AD	Large-AD vs. small-ab	Large-ab vs. small-AD	Large-ab vs. small-ab	small-AD vs. small-ab
Stomata/cm^2		-	-	-	-	-	-
Trichomes/cm^2		-	-	-	-	-	-
Stomata/trichome		-	-	-	-	-	-
Stomatal length		+	+	+	+	+	-
Stomatal width		-	+	+	+	+	-
Stomatal length/width		-	+	-	-	-	-
Glandular trichomes, % of those counted		-	-	-	-	-	-

[a]Key for the symbols and abbreviations used in the above table.

Confidence level	Leaf surface
- 98% or above	AD - adaxial
- below 98%	ab - abaxial

Fig. 3-6. Leaf transections of four species of *Abronia* showing arrangement and dimensions of three tissue regions: spongy and palisade parenchyma, vein extensions, and vascular bundles. All figures are enlarged to scale. —3. A. *alpina*. —4. A. *villosa* var *aurita*. —5. A. *maritima*. —6. A. *nana* ssp. *covillei*.

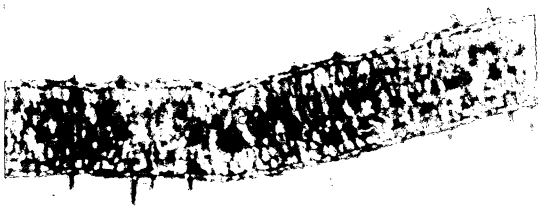


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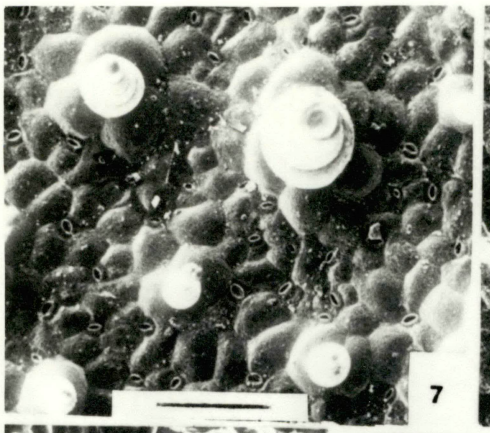
Fig. 7-14. SEM micrographs of adaxial and abaxial leaf surfaces of four species of *Abronia* illustrating relative stomatal and trichome densities. Line represents a scale of 0.1 mm. —7. A. *villosa* var *aurita*, adaxial surface. —8. A. *villosa* var *aurita*, abaxial surface. —9. A. *nana* ssp. *covillei*, adaxial surface. —10. A. *nana* ssp. *covillei*, abaxial surface. —11. A. *maritima*, adaxial surface. —12. A. *maritima*, abaxial surface. —13. A. *alpina*, adaxial surface. —14. A. *alpina*, abaxial surface.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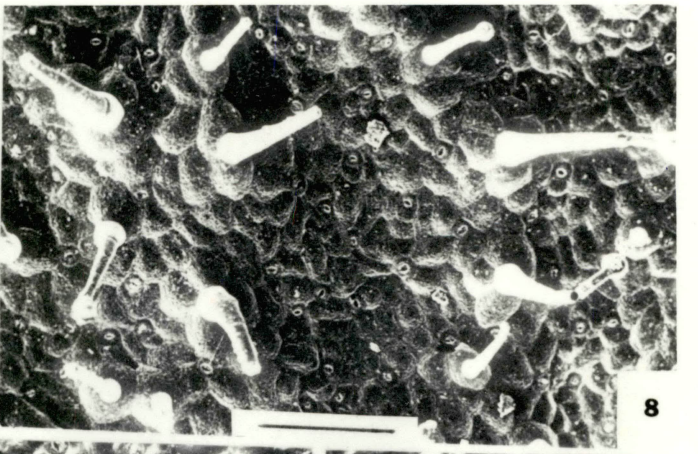
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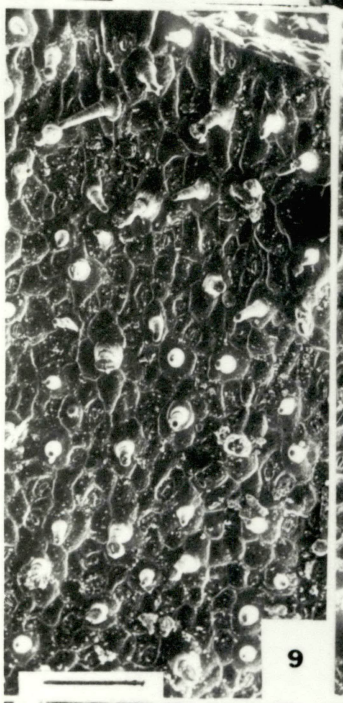
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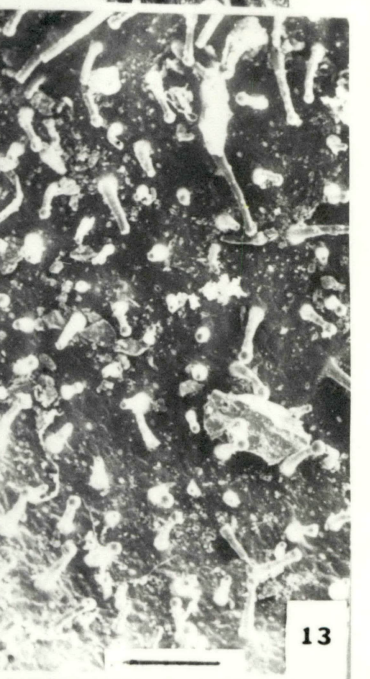
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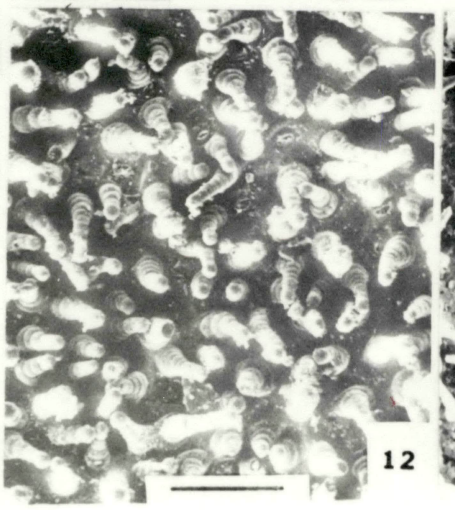
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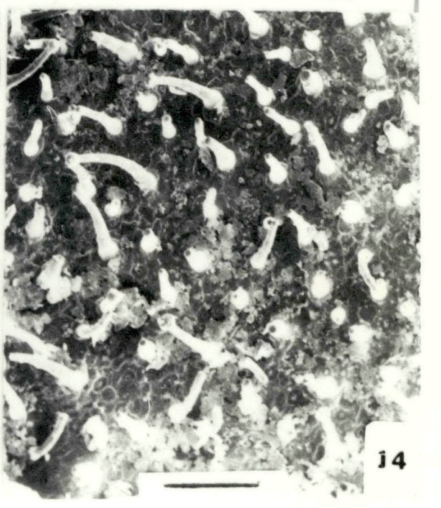
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Fig. 15-19. SEM micrographs of leaf surfaces of four species of *Abronia* illustrating the morphological diversity of trichomes. Line represents a scale of 0.1 mm. —15. A. *villosa* var *aurita*, adaxial surface. —16. A. *villosa* var *aurita*, abaxial surface. —17. A. *maritima*, adaxial surface. —18. A. *nana* ssp. *covillei*, adaxial surface. —19. A. *alpina*, adaxial surface.

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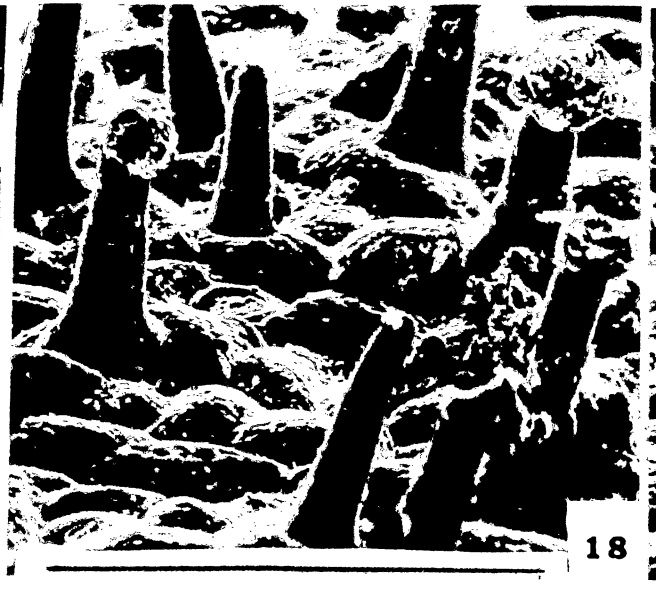

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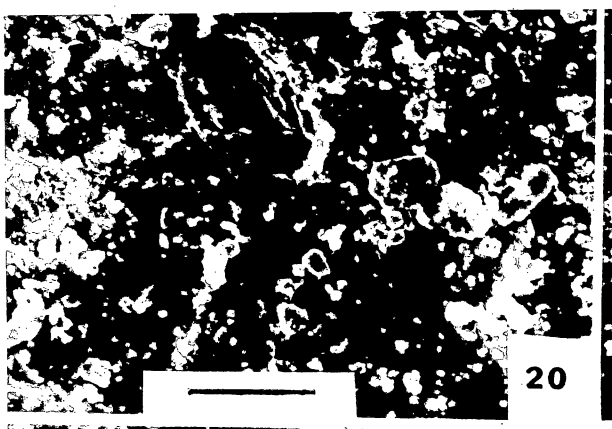
Fig. 20-27. SEM micrographs of stomata from species of *Abronia*. Line represents a scale of 10μ. —20. A. *alpina*, adaxial surface. —21. A. *alpina*, abaxial surface. —22. A. *nana* ssp. *covillei*, adaxial surface. —23. A. *nana* ssp. *covillei*, abaxial surface. —24. A. *villosa* var *aurita*, adaxial surface. —25. A. *villosa* var *aurita*, abaxial surface. —26. A. *maritima*, adaxial surface. —27. A. *maritima*, abaxial surface.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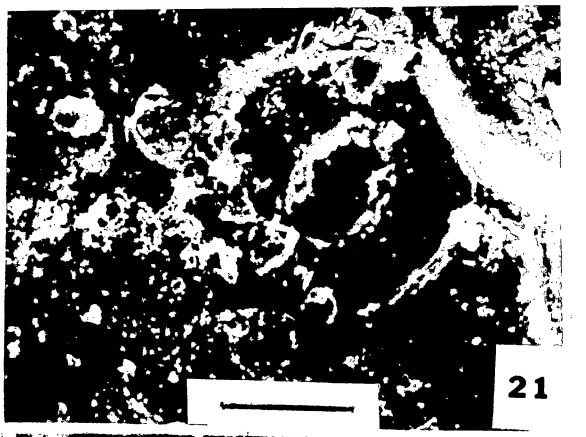
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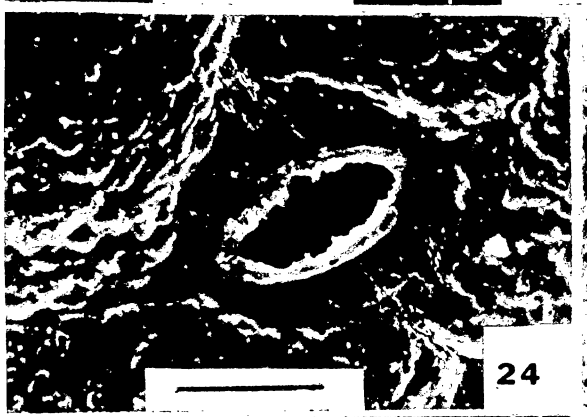
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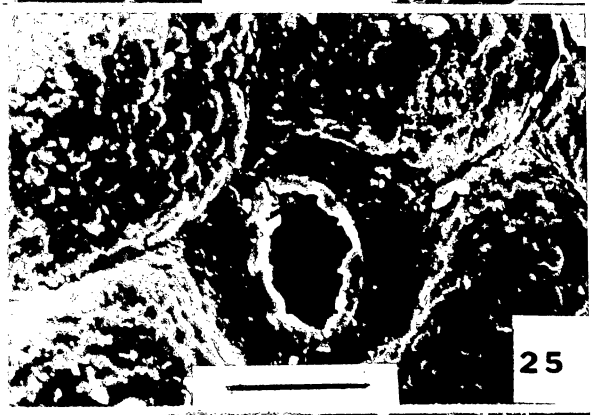
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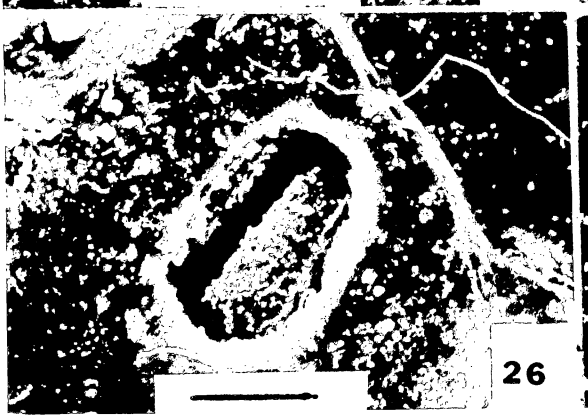
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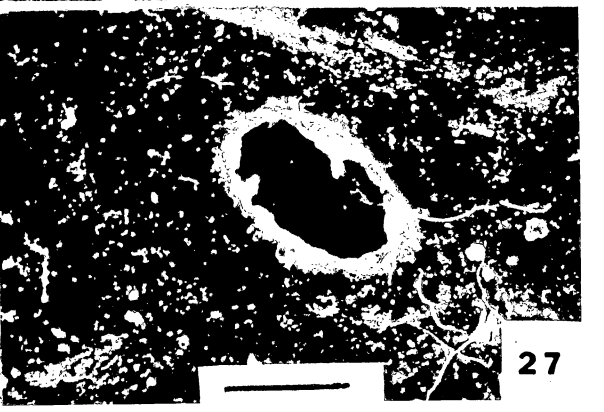
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DISCUSSION

The degree of adaptive variability is confined within the limitations of the genetic capabilities of individual species, therefore, a study of adaptive mechanisms is particularly meaningful when limited to a small taxonomic group such as a genus or species (Keller 1925).

Environmental conditions of high light intensity, low rainfall, sustained hot or cold temperatures, and nutrient or water deficiency brought upon by porous, well-drained soils, can produce anatomical and morphological modifications classified as xeromorphy. Although members of the genus *Abronia* are probably not xerophytes in the strictest sense (Maximov 1931), they do exhibit some modifications common to the syndrome of xeromorphy. The most common xeromorphic features are reduced leaf surface area, strongly developed palisade tissue, decreased epidermal and palisade cell size, increased frequency and size of vascular bundles, and a notable increase in stomatal and trichome frequencies (Mortenson 1973).

A high stomatal frequency, coupled with an increased transpiration rate when abundant water supply is present, is considered an important xeromorphic character by many researchers (Shields 1950, Wylie 1943, Shah and Kothori 1975).

Penfound (1931) showed that the stomatal frequency of *Helianthus annuus* L. increased by 50% in dry soils and 33%

in moist soils when compared to wet soils. This appears to be contradictory to the theme of water conservation, but it is not the rate of transpiration when water is available, but rather the ability to reduce water loss to a minimum in times of water shortage that characterizes xerophytes (Maximov 1931).

According to Coulter, et al. (1931), in 200 genetically distinct groups the same individual plants produced a more xerophytic leaf type in an alpine region than in lowlands. The porous, well-drained soils, accompanying cold temperatures, and low humidity found within the alpine environments is probably responsible for the high stomatal frequency found for *Abronia alpina* leaves in this study (Table 8). The desert environment of *Abronia villosa* var *aurita* is more xeric than the montane environment of *Abronia nana* ssp. *covillei* or the coastal habitat of *Abronia maritima*. *Abronia villosa* var *aurita* has a correspondingly higher stomatal frequency (Tables 5, 6, & 7). Although A. *nana* ssp. *covillei* is montane, it is not subjected to the harshness of the alpine or desert environments due to the sometimes frequent summer rains and lower temperature fluctuations. The fore-dune habitat of A. *maritima* is subjected to mild temperature fluctuations, higher humidity, and lower light intensity than is found in the other habitats. *Abronia maritima* has correspondingly the lowest stomatal frequency (Table 5).

In some cases, a high stomatal frequency is reported

to be a secondary manifestation of a decrease in epidermal cell size (Lea, et al. 1977). This is partially true for A. *alpina*, but not for A. *villosa* var *aurita*, which has the second highest stomatal density but not a correspondingly small epidermal cell size (Tables 2 & 3).

Stomatal density is also influenced by leaf position and surface orientation. Stomatal density is reported to decrease with each subsequent lower leaf insertion on the culm of *Triticum aestivum* (Teare, et al. 1971). Stomatal frequencies are usually greater on the abaxial surface of a leaf, and in extreme cases are totally absent from the adaxial surface (Ghose and Davis 1973). Orientation of leaf surfaces does not affect stomatal densities of *Abronia* species however, because there is no appreciable difference in stomatal frequencies of either abaxial or adaxial surfaces (Tables 10 & 11).

There appears to be some correlation between stomatal density and stomatal size within small leaves of some *Abronia* species. *Abronia alpina* has the highest stomatal density as well as the smallest stomata, followed by A. *villosa* var *aurita*, which has the second highest stomatal density and correspondingly the second smallest stomata (Tables 6 & 8). According to Penfound (1931), stomatal size varies the same direction as soil water content, contrary to Sharma (1972), who found stomatal dimensions to be the largest within plants from the more xeric soils. No trend is apparent correlating environmental conditions with stomatal sizes for the *Abronia* species

studied.

Regarding subsidiary cells, dicotyledons show four principal stomatal patterns; anomocytic, anisocytic, paracytic, and diacytic (Esau 1960). Shah and Kothori (1975) described approximately eleven stomatal pattern combinations within the family Papilionaceae, and stated that in some cases different patterns are found adjacent to each other on the same leaf surface. Because of the variability of stomatal patterns, there does not appear to be a pattern "type" which has adaptive advantages for a particular environment. The leaves of *Abronia* species have no apparent subsidiary cell development in conjunction with the stomata, and therefore their stomatal pattern is anomocytic.

The ecological significance of a pubescent surface is ambiguous, and the literature contains a wide spectrum of studies correlating trichomes to both abiotic and biotic parameters.

Shields (1950) speculated that trichomes were a ramification of water loss by epidermal cells, while (Shields and Mangum 1954) noted that the low nitrogen soil content enhanced trichome development. Yapp (1912) demonstrated that the leaves of *Spiroea ulmaria* L. became 37% warmer when trichomes were removed. Yapp's (1912) work corroborates a study by Wolpert (1962) who discusses the significance of trichomes as structures from which heat can be dissipated by conduction and convection.

Trichomes are thought to influence transpiration rate. Gates (1968) speculated that a trichome cover would reduce transpiration by increasing the boundary layer of resistance surrounding the stomata. This would be accomplished by decreasing the amount of free air flow over the stomata. Hendryey (1967) noted an increase in the transpiration rate for the leaves of *Verbascum thapsus* L. when the trichome was removed. Contrary to the theme of water conservation, Shapiro and De Forest (1932), and Sayre (1920) noted that more pubescent species have a higher transpiration rate. Thut (1938) proposed that trichomes could possibly act as a device for water absorption while Woolley (1964), showed that a significant degree of transpiration can occur within the actual trichome surface. Trichomes in the latter case would be detrimental to water conservation. Aside from functioning as a device to modify the leaf's physical environment, trichomes can possibly alter the biotic environment by acting as a barrier to insect foraging Levin (1973).

High temperature, high sunlight, dry soils, and low humidity promote the greatest trichome development, while environments characterized by filtered sunlight and high humidity have a low trichome frequency (Sharma 1972 and Hsiao 1973). Coulter, et al. (1931) noted that where a single species exists in both mesic and xeric habitats, the plants found in the xeric habitats are more pubescent. Johnson (1975) indicated that the state of maturity of the foliage plays a

part in the relative trichome density. The more mature foliage becomes more dense in the dryer environments, while the immature foliage had the highest trichome production in the mesic environment.

Recent studies on leaves of *Acer saccharum* Marsh by Sharma (1975 a) and *Plantago lanceolata* L. by Sylvia (1975), show that environmental pollution resulted in an increase in trichome production.

If an increasing trichome density is an indicator of increasing xeromorphy, the leaves of *Abronia* species studied appear to contradict this trend. *Abronia maritima*, the species from the least xerophytic environment, has the highest trichome density while the alpine and desert species A. *alpina* and A. *villosa* var *aurita*, have the lowest trichome densities (Tables 5-8, Fig. 7-14). Perhaps there is a correlation between trichome frequency and trichome size. *Abronia villosa* var *aurita* has the lowest trichome density but has overwhelmingly the largest trichomes (Table 2). This correlation does not appear valid for A. *alpina* (Tables 4 & 8, Fig. 13 & 14) and A. *nana* ssp. *covillei* (Tables 3 & 7, Fig. 9 & 10), because their trichome frequencies are not inversely related to their trichome size.

All species of *Abronia* studied have uniseriate trichomes with a significant percentage being capitate or glandular (Tables 5-8). Each species has a trichome structure which is unique for that particular species. No two species

have the same trichome morphology. For the species *A. maritima*, *A. nana* ssp. *covillei*, and *A. alpina*, there is little or no diversity among trichomes found on any individual leaf surface, as well as no diversity between trichomes found on abaxial and adaxial leaf sides (Fig. 15-19). However, for the species *A. villosa* var *aurita*, there is diversity among trichomes found on any individual leaf surface, and a marked difference in trichome morphology between abaxial and adaxial sides. The trichomes on adaxial leaf surfaces have a significantly larger base than trichomes on abaxial surfaces (Fig. 15 & 16). The enlarged adaxial trichomes might aid in protecting the leaf from damage due to intense sunlight and wind desiccation.

The percentage of trichomes having glandular structures seems to be species specific. Almost 90% of the trichomes of *A. villosa* var *aurita* are glandular, followed by *A. alpina*, *A. nana* ssp. *covillei*, and lastly *A. maritima*. Therefore, size and presence of glandular trichomes may compensate for low numbers.

The presence of glandular trichomes might be a deterrent to insect foraging (Levin 1973).

An interesting correlation exists between the densities of stomata and trichomes for the *Abronia* species. The ratio of relative numbers of stomata to trichomes is constant and particular for each species, despite fluctuations in densities of trichomes or stomata for any given leaf surface

(Tables 5-8). Any change in the density of stomata for a leaf surface is followed by a reciprocal fluctuation in trichome density, which results in the same stomatal/trichome ratio particular for that species. This seems to indicate that there is a significant relationship between the stomatal and trichome structure. Their relative numbers are controlled by some regulatory mechanism, which is probably influenced by both biotic and abiotic parameters. Studies of stomatal and trichome relationships are generally lacking in the literature.

Palisade cell development at the expense of spongy mesophyll is an important xeromorphic feature (Shields 1950). Palisade parenchyma tends to be cylindrical in shape and elongated perpendicular to the epidermis, and consequently has limited lateral contact. The perpendicular stature of palisade cells complicates the conduction of solutions in the plane parallel to the leaf blade, requiring up to 10 times as many cells when compared to an equal distance for spongy mesophyll (Wylie 1939). Therefore to facilitate proper conduction of solutions within palisade tissue, vascular bundles tend to be larger and closer together.

Palisade cell structure presents a significantly greater amount of intracellular space when compared to spongy mesophyll cells, and coupled with a higher chloroplast content partially explains the higher photosynthetic and transpiration rates for leaves having pronounced palisade cell development (Thoday 1931).

The increased development of palisade tissue at the expense of spongy tissue is an indicator of xerophytic modification for A. *alpina* (Table 4, Fig. 3), A. *villosa* var *aurita* (Table 2, Fig. 4), and A. *nana* ssp. *covillei* (Table 3, Fig. 6), while A. *maritima* (Table 1, Fig. 5) has a significant development of spongy mesophyll indicative of a more mesophytic leaf type.

Epidermal cell dimensions are generally reduced within leaves from the more xerophytic environments. However, there is an increase in epidermal cell thickness with increasing light intensity (McCree and Davis 1974). The adaxial epidermal cells within xerophytic leaves tend to be thicker than the abaxial epidermal cells, and this modification offers more protection from possible damage due to intense irradiation.

The adaxial epidermal cell dimensions are largest for leaves of A. *villosa*, followed by A. *maritima*, A. *nana* ssp. *covillei*, and A. *alpina* (Tables 1-4).

The leaves of A. *villosa* var *aurita* lie prostrate and are more directly exposed to sunlight than the elevated leaves of A. *nana* ssp. *covillei* and A. *alpina*, suggesting that the adaxial epidermal cells of A. *villosa* var *aurita* are modified to a greater degree. The abaxial epidermal cells are largest for A. *maritima*, followed by A. *villosa*, A. *nana* ssp. *covillei* and A. *alpina*. The larger epidermal cells of A. *maritima* are attributed in part, to the general increase in cell size

within plants that occupy less xeric habitats. The leaves of *Abronia* species follow the trend that adaxial epidermal cells are larger in dimension than the abaxial epidermal cells.

A very important tissue system within the leaf is the vascular system, and its character is also influenced by environmental conditions. There is an increase in the frequency and overall vascular bundle dimensions within leaves from the more xeric habitats (Mortenson 1973).

The organization of the vascular tissue is directly related to the organization of the nonvascular tissues within the leaf. The epidermal and spongy mesophyll layers constitute a system which supplements lateral transfer of materials, while the palisade tissue offers a substantial resistance to material transfer. Therefore, the relative degree of development of these tissues significantly influences the nature of the vascular tissue within the leaf (Wylie 1939).

The vascular bundles of A. *maritima* are significantly larger in dimension than in the other three species, which is possibly due to an increased conduction requirement of a substantially larger leaf. The vascular bundles of A. *nana* ssp. *covillei* small leaves are slightly larger than the vascular bundle of A. *villosa* var *aurita* small leaves, while the converse is true for the large leaves of these species. The palisade development of these species is very similar, which in part explains the similarity of their vascular bundle dimensions (Tables 1-4, Fig. 3-6).

In addition to major and minor vascular bundles, there is a supplemental conduction system of vein extensions. Vein extensions occur on portions of the major veins within *Abronia*, and probably supplement vertical transfer of materials from the bundles to the epidermis. The vein extension could possibly be an additive support tissue which operates on hydraulic pressure (Wylie 1943). Vein extensions occur to a large extent within the leaves of A. *villosa* var *aurita*, A. *nana* ssp. *covillei*, but occur to a lesser degree within the leaves of A. *maritima* (Fig. 3-6). The leaves of A. *maritima* have in some cases a significant spongy mesophyll development, and in these leaves there is no appreciable development of vein extensions. In this case, spongy mesophyll provide an adequate system of vertical conduction as well as support between the epidermal layers.

SUMMARY

Anatomical and morphological modifications seen within the leaves of the four species of *Abronia* studied are correlated with ecological differences of their habitats. The anatomical and morphological modifications are considered to be an integral part of the adaptive process *Abronia* species have undergone within their ecologically distinct habitats.

The maritime species, *Abronia maritima*, has a leaf structure indicative of a plant occupying a mesophytic habitat. Low stomatal densities coupled with the larger size of most major anatomical characters including palisade cell height and width, vascular bundle height and width, and large well developed spongy mesophyll cells constitute a mesophytic leaf structure. Mild temperatures, high humidity, and frequently filtered sunlight are environmental parameters classifying the coastal fore-dune habitat as being mesophytic.

The cold temperatures, intense sunlight, and low humidity of the alpine environments coupled with the granitic, well-drained soils are directly correlated to the xerophytic leaf structure of *Abronia alpina*. A universal reduction in size of major anatomical characters, the large relative amount of palisade parenchyma, and a very high stomatal density are modifications found within leaves of plants

occupying a xerophytic habitat.

The desert species *Abronia villosa* var *aurita* and the montane species *Abronia nana* ssp. *covillei* have leaf anatomy which is similar and also characteristic of plants occupying xerophytic habitats. Reduced size of major anatomical characters, high stomatal densities, and a well developed palisade tissue with a diminutive amount of spongy parenchyma occurs within the leaves of both species. Therefore, the leaves of A. *villosa* var *aurita* and A. *nana* ssp. *covillei* are also classified as being xerophytic, but to a lesser degree than the leaves of A. *alpina*.

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